

THE MOVEMENTS AND INNERVATION
SMALL INTESTINE. BY W. M. BAYLISS AND E. H.
STARLING. (Eleven Figures in Text.)

Reprinted from the Journal of Physiology.
Vol. XXVI. Nos. 3 & 4, February 28, 1901.

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THE MOVEMENTS AND INNERVATION OF THE
SMALL INTESTINE. BY W. M. BAYLISS AND E. H.
STARLING. (Eleven Figures in Text.)

(From the *Physiological Laboratory, University College, London*.)

IN a previous paper under the above title, we dealt only with the small intestine of the dog. It was of considerable importance to extend these observations to other animals in order to ascertain whether the conclusions arrived at in the first paper held good only for the dog or whether they were of general application.

II.

THE SMALL INTESTINE OF THE RABBIT.

Methods. The methods adopted in the investigation of the movements of the rabbit's small intestine were very similar to those adopted in our previous research. We found however that the wall of the rabbit's intestine was at the same time too delicate and too excitable to give any reliable results with the enterograph, so that all our tracings were obtained by the insertion of a rubber balloon in the lumen of the gut. This was distended with air under the pressure of about one inch of water, and connected with a piston recorder. The much greater excitability of the rabbit's intestine as compared with that of the dog, and the mode of its contraction may render the balloon method unreliable unless controlled by ocular inspection. At the same time the spontaneous variations in the activity of the gut renders the method of simple inspection in many cases misleading, although observations of this character have the advantage that they can be carried out without the introduction of an abnormal irritant like the balloon into the lumen of the intestine.

Behaviour of the enervated intestine. Local reflexes.

In order to cut off the intestines from the influence of the central nervous system, both vagus nerves were divided, and the spinal cord

destroyed by pithing from the 4th or 5th dorsal nerve downwards. In some cases, both splanchnic nerves were divided in addition, but this was subsequently found to be unnecessary. The animal was then placed in a bath of warm normal saline, the abdomen opened, and the intestines allowed to float freely in the bath.

In animals treated in this way, the intestines on exposure are found to be in a state of great activity, the writhing "pendulum" movements being especially well marked. In addition to these movements, true peristaltic contractions may often be observed at several points of the gut. Where these are going on, the gut is constricted to a cord and blanched over a length of 1 to 3 cm. This constriction advances slowly down the intestine driving before it intestinal contents and air, which bulge out the walls of the intestine below the constriction. On pinching the intestine at any spot, the excitation is seen to spread upwards and a constriction is produced which, at first at any rate, is most marked about 1 or 2 cm. above the stimulated point. An inhibition below the stimulated spot is not very apparent. A short distance below the writhing movements may be as pronounced as in any other portion of the gut. The same ascending excitation may be produced, as was shown by Nothnagel, by the direct application of a crystal of common salt to the external surface of the intestine. In some cases, in consequence of the use of too much force in stimulating or of the presence of some irritating material in the lumen of the intestine, a constriction which lasts a considerable time may occur just above the excited spot. This constriction is not inhibited as a rule by stimulation of the intestine above. Descending waves of constriction pass down and die away just above the permanently constricted ring.

If a bolus of cotton wool and vaseline or a distended balloon be inserted into the gut, it is rapidly driven down. This movement is effected by an advancing wave of constriction, which is most marked at about 1 or 2 cm. above the bolus. In the region of the bolus itself, the gut is generally relaxed, and the state of relaxation must extend a short distance below. Thus if the balloon be connected with a piston recorder, it may be rapidly driven along the intestine without any sign of intestinal contraction being displayed on the tracing. The longitudinal fibres of the gut seem to take a prominent part in the peristalsis. The intestine appears to be drawn over the bolus by the contraction of the longitudinal fibres above, the amount of force spent on driving on the bolus being apparently only small. If the bolus in its course arrive at a region where the gut is constricted from continual irritation, its

progress is stayed, and the wave of contraction either dies away or more generally passes over the bolus to the constricted ring. The same thing occurs if the onward progress of the bolus be prevented in any way, the wave passing over the bolus and down the intestine below it.

Thus from simple inspection we may conclude that the intestine is the seat of two kinds of contractions—rhythmic contractions giving rise to the pendulum movements and running rapidly down the intestine, and slow peristaltic waves generally evoked by some special stimulus. The latter are evidently due to an excitation which spreads up the intestine from any excited spot. The evidence of a descending inhibition is, however, less marked, although in the normal gut the advancing wave of constriction is always preceded by a short length in which the intestine is distended by air or other contents.

These conclusions are borne out by an investigation of the activity of the intestine by the graphic method.

Intestinal rhythm. The intestinal wall separated from the central nervous system is constantly the seat of rhythmical contractions occurring 10 to 12 times a minute, and apparently involving both muscular coats, although we could not definitely ascertain this point by means of the enterograph. As in the dog, these contractions are increased in amplitude within limits by increased tension and in rhythm by increasing the temperature of the bath. They occur in the excised intestine long after all traces of local reflexes have disappeared, and are probably to be regarded, like the similar contractions of the dog, as myogenic.

Local reflexes. The ascending excitation, as the result of a local stimulus, either a pinch, or a sudden distension of the balloon, or the application of sodium chloride, is always well-marked and easy to evoke. In the experiment from which Fig. 1 is taken, two balloons were placed in a loop of the small intestine, their ends being 2 cm. apart. The upper balloon was connected with the piston recorder, and was maintained at a constant moderate distension. The lower balloon could be distended at will by the injection of fluid into it. It will be seen that the first distension caused simply a slight augmentation of the contractions of the intestine in the neighbourhood of the upper balloon, whereas a second longer distension caused a strong tonic contraction with rhythmic intermissions. On inspection this contraction was seen as a broad constricted band which did not die away but passed over the balloon and down the intestine. This ascending excitation generally first takes effect over 2 or 3 cm. of the gut above the stimulated point.

In no case have we observed a spread of excitation more than 5 or 6 cm. above the stimulated spot.

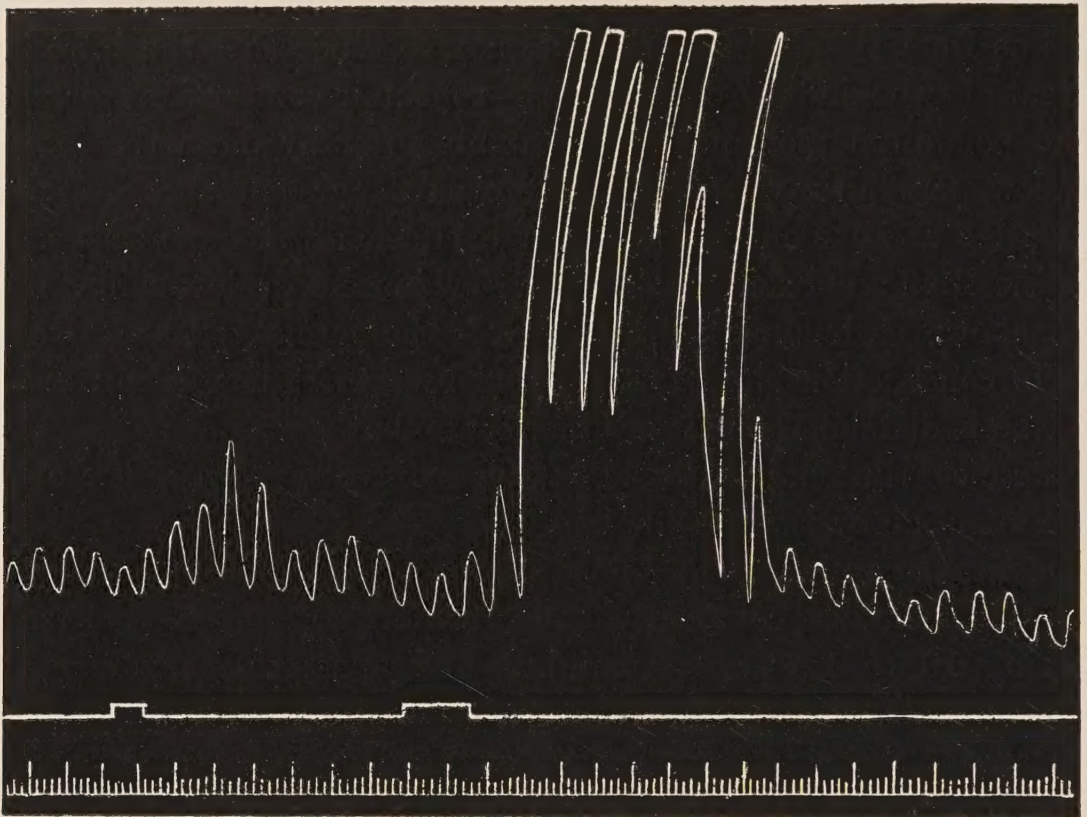


Fig. 1. Tracing of intestinal contractions, showing the effect of distension of the wall of the gut below the recorded spot.

As we should expect from our experiences with the inspection method, the descending inhibition, as the result of local stimulation, is very much less marked than in the case of the dog. In some cases it is impossible to elicit any relaxation of the gut in the neighbourhood of the balloon by the application of a stimulus higher up, the normal stimulus, due to the presence of the balloon, being more than sufficient to counteract the descending inhibitory impulses. But we have observed this inhibition sufficiently often to learn something of its peculiarities. It never extends down the intestine more than 3 or 4 cm., *i.e.* about the space occupied by the bubble of gas which precedes each peristaltic wave to be observed in the freshly exposed gut.

Not only is the inhibition limited in extent; it is also limited in time. A short stimulus causes in the gut immediately below a diminution of tone with a dropping or decrease of one or two beats (Fig. 2). A continuation of the stimulus is without effect in prolonging the inhibition. In fact, in many cases the contraction excited above the

stimulated spot extends over this spot and travels down the intestine, so that a record of the intestinal contractions below the point of

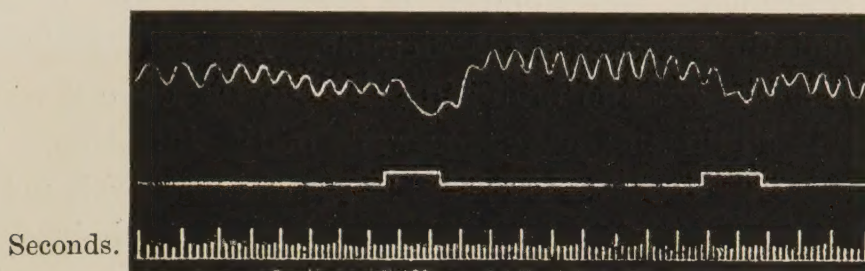


Fig. 2. Tracing of intestinal contractions, showing temporary inhibition as a result of pinching intestine above recorded spot.

excitation shows a temporary slight inhibition followed by a strong contraction (Fig. 3).

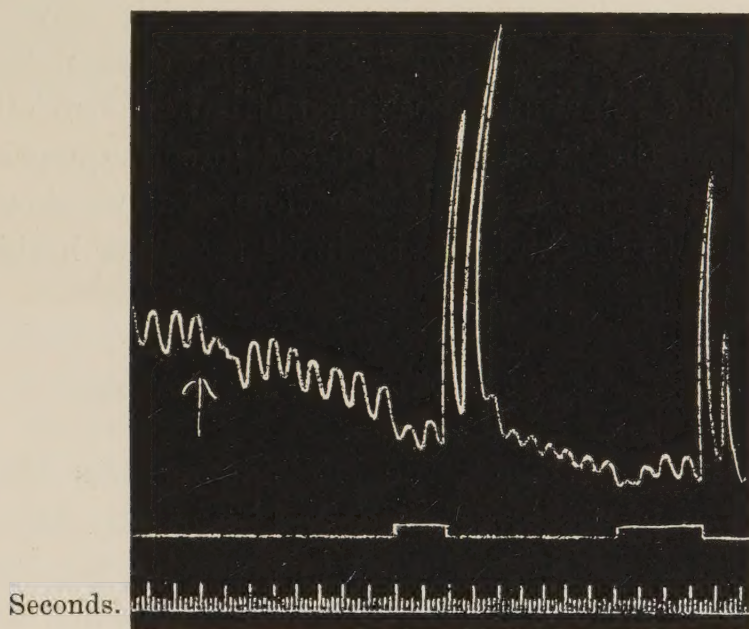


Fig. 3. Tracing to show effects of pinching above balloon. A temporary inhibition is followed by excitation propagated from above excited point. (Middle line shows duration of stimulation.)

We thus see that fundamentally the activity of the rabbit's intestine resembles that of the dog's. In each case local stimulation causes excitation above and inhibition below the excited spot. The differences between the intestine in the two cases are of degree only, and are probably intimately connected with the different alimentary conditions of the two animals. In the dog the intestine is short and thick-walled. A strong peristaltic wave could empty practically the whole small intestine. The amount of contents in the alimentary canal is never

very large, and long periods occur during which the intestines are practically empty. In a herbivorous animal, such as the rabbit, feeding is almost continuous, the stomach is always full, the intestines are very long and their contents considerable. A single peristaltic wave sweeping down the gut and inhibiting all activity before it would throw a considerable strain on the tender walls of the intestine. These are saved, as we have already shown, by being pulled in a relaxed condition over the bolus. There is no forcible pushing of the bolus against the resistance of the intestinal wall. This mode of passage of contents along the intestine would be clearly inapplicable to a great mass occupying perhaps 2 or 3 feet of gut. Hence peristalsis in the rabbit's intestine is made more discrete, each segment of gut moving on the contents which may happen to be in it, without reference to what is going on in the intestine above or below. A clashing of activities of various parts can hardly occur, since a peristaltic wave, driving an easily moving bolus against a constricted ring does not inhibit this latter, but the bolus remains in position until the constriction below it has passed on down the intestine, or relaxed in consequence of removal of its exciting cause. It is probable, therefore, that we should find very similar conditions of intestinal activity in all the other herbivora.

Extrinsic innervation of the intestines.

In the rabbit as in the dog, the intestine receives fibres from the sympathetic through the splanchnic, and from the two vagi. The action of these nerves has been studied by observing the effects of their excitation on the activity of a loop of intestine in which a balloon was inserted, the balloon being connected with a piston recorder.

Action of splanchnic nerves. Although various authors have described motor effects as resulting from the stimulation of the splanchnic nerves both in the dog and in the rabbit, we have been unable in either of these animals to obtain anything except purely inhibitory results, and are inclined, therefore, to ascribe the motor results obtained by other observers either to faulty methods of experiments, or to a mistaking of the resumption of the normal activity at the cessation of stimulation to the effects of the stimulus itself. In Fig. 4, we give a tracing of such an inhibition resulting from the stimulation of the left splanchnic nerve in the rabbit, with a moderate faradic current. In this, as in all other experiments, the cord was destroyed from the 5th dorsal nerve

downwards, and both vagi divided in order to avoid any central or reflex variations of intestinal activity.

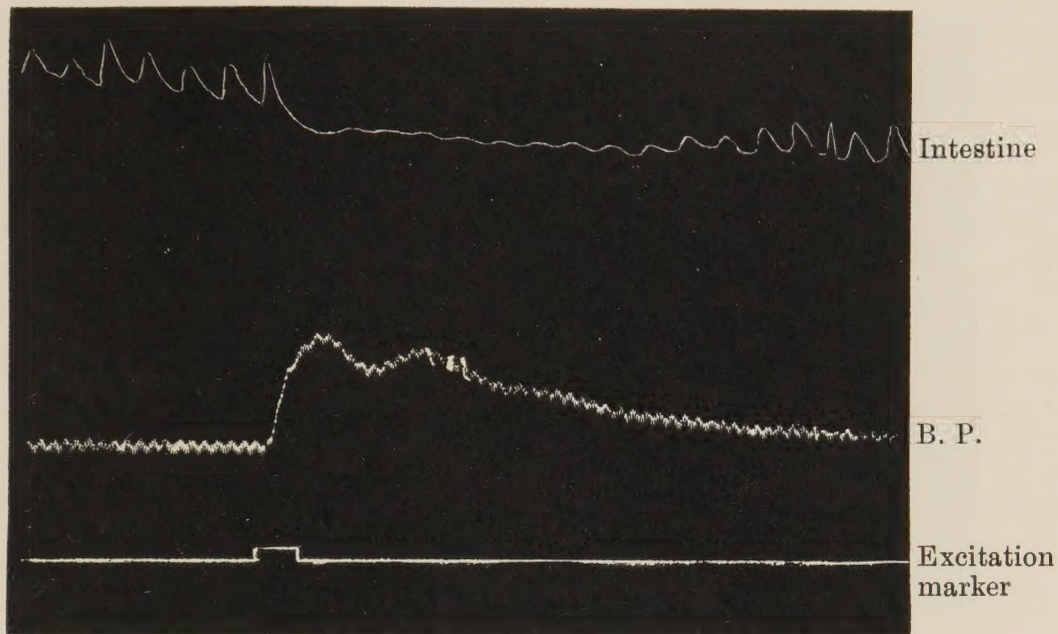


Fig. 4. Tracing to show effect of splanchnic stimulation.

Exactly the same effect may be produced by stimulation of the mesenteric nerves, and may be often obtained by exciting these nerves several minutes after the intestine has been cut out of the body, showing its independence of the coincident vascular effects of splanchnic excitation. So far as we could make out, the relaxation affected both coats equally. On no occasion could we detect a shortening of the intestine as the result of splanchnic stimulation. The inhibition affects all parts of the small intestine alike, and abolishes for a time not only the rhythmic myogenic contractions, but also any peristaltic constrictions which may be present at the moment of stimulation.

Influence of the vagi. The augmentor effect of the vagi on the intestinal movements was first observed in the rabbit, and has, we believe, never been denied for this animal. It is obtained with much greater ease than in the dog and is often observed the first time that the vagus is stimulated. Both vagi are equally effective (Fig. 5.) On inspection, all parts of the small intestine are influenced in the direction of increased activity, although the increase is more marked in the neighbourhood of the recording balloon or the seat of any special stimulation. There is one striking difference between the vagus action in the rabbit and in the dog. In the former animal, there is no trace of the preliminary inhibition, which is so constantly observed as the

result of stimulating the vagus in the dog. Since the rabbit's intestine differs from that of the dog chiefly in the very limited extent of the

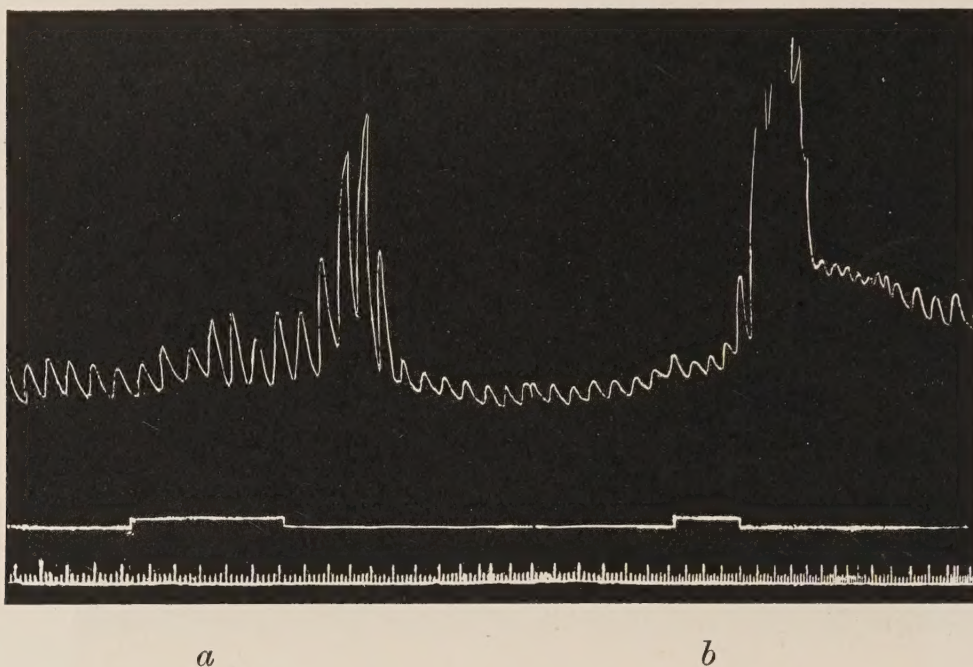


Fig. 5. Tracing to show effect of excitation of vagus on intestinal activity. At *a* the right vagus, and at *b* the left vagus was excited.

descending inhibition resulting from the local stimulus, we are inclined to regard the preliminary inhibition occurring in the dog, not as the direct result of stimulating inhibitory fibres in the vagus, but as the consequence of a state of excitation occurring higher up in the alimentary canal. This view however we would put forward with some reserve, since we may sometimes obtain a well-marked preliminary inhibition as the result of stimulation of the vagus in the cat, although in the same experiment it may be impossible to elicit any form of local reflex, either ascending excitation or descending inhibition. (See next Section.)

The greater ease of obtaining vagus augmentor effects in the rabbit as compared with the dog seems to be merely a part of the general preponderance of the motor activities of the gut in the former animal.

Effect of anæmia. It is a common experience that cessation of the circulation in the rabbit causes increase of the intestinal movements, so that in a recently killed animal, for example, these organs are found, on opening the abdomen, to be in a state of great activity. In this respect there is a marked difference between the rabbit and the dog, where death of the animal is followed almost at once by a cessation of all intestinal movements. We were surprised therefore, on investigating

the effect of anæmia on the enervated intestine, to find that, although less marked than in the dog, it was in the same direction, *i.e.*, of diminished activity. (Fig. 6.)

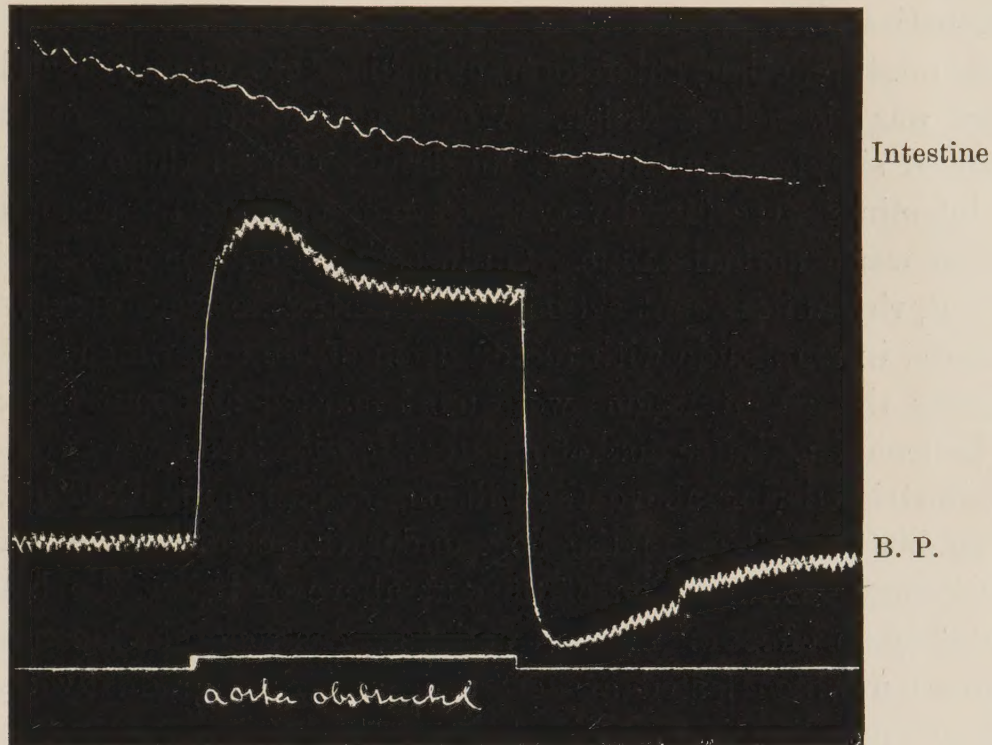


Fig. 6. Effects of anæmia (aortic obstruction) on activity of enervated intestine.

We are therefore inclined to ascribe the post-mortem activity of the intestines in the rabbit, not to the anæmia or asphyxia of the intestinal wall, but to the paralysis of the nerve-centres, and the consequent cutting off of the intestines from all inhibitory impulses. It is quite possible, as Engelmann suggests, that when the vagi are intact we have superadded a distinct motor effect due to central stimulation of these nerves resulting from the asphyxia. In a rabbit, with all the nerve-connections of the intestine intact, cutting out a loop of intestine increases for a time its activity, and in such a loop it may for a time be possible to elicit local reflexes which could not be obtained with the intestine *in situ*.

III.

THE SMALL INTESTINE OF THE CAT.

The similarity between the intestine and alimentary habits of the dog and cat led us to anticipate that we should find a very exact correspondence between the properties of the intestines of the two animals. We were much surprised to find in the majority of our expe-

riments a total absence of all local reflexes. In these experiments the enervation was effected either by destruction of the spinal cord from the 4th dorsal nerve downwards, or in most cases by an extirpation of all the ganglia and nerve-fibres lying on the abdominal vessels. The anæsthetics were varied from experiment to experiment. In turn, A.C.E. mixture, ether, chloroform, morphia, were employed and in some curare was given in addition. We also tried the effect of anæsthesia produced simply by cutting off the brain. In all these cases however, the intestines were found very inactive on opening the abdomen in the bath of warm normal saline. On inserting a balloon into the lumen of the gut, rhythmical contractions of the intestine were observed, which increased in amplitude with the duration of the experiment. In nearly all cases these contractions were most marked at about the centre of the balloon, *i.e.*, the region of greatest tension; and we did not notice the constricted ring above the balloon, which is so marked a feature in the rabbit as well as in the dog, under the conditions of our former experiments. Stimulation of the gut above or below the balloon had absolutely no effect on the contractions. A strong pinch caused a local contraction which lasted a short time and then gradually died away, without spreading in one direction or the other.

On extending our observation to kittens, the same inexcitability of the local nervous system was observed. One of these experiments however showed us that the local reflex mechanism was in abeyance

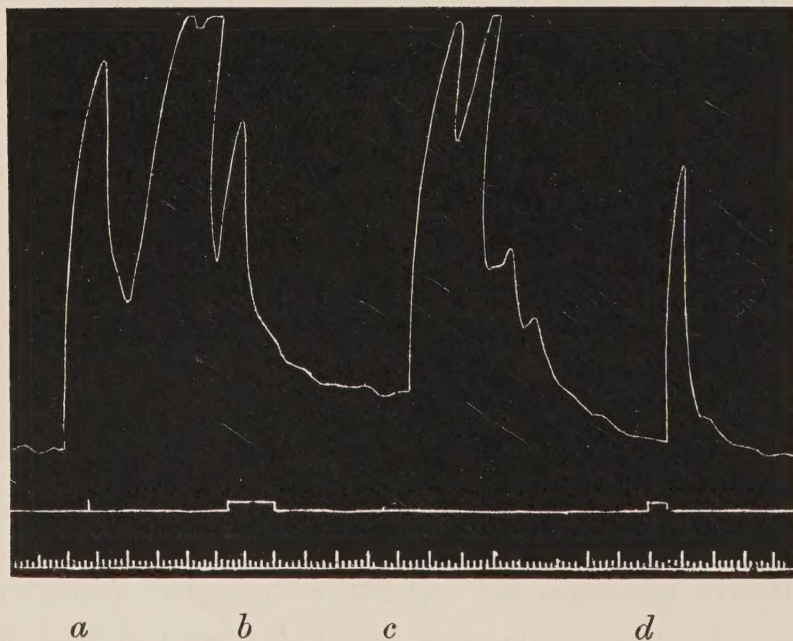


Fig. 7. Local reflexes in kitten's intestine, after asphyxia. At *a*, *c*, *d*, the intestine was pinched *below* the balloon. At *b* the pinch was applied *above* the balloon.

rather than absent. At the end of the experiment, the kitten, which had ceased to breathe spontaneously, was allowed to die of asphyxia. Five minutes afterwards the intestine was again stimulated below the recording balloon, and was now found to give a well-marked local reaction. (Fig. 7.) The intestine, which was previously at rest, contracted forcibly in the neighbourhood of the balloon each time the intestine was pinched 2 cm. lower down. A descending inhibition was apparently also to be obtained in this case but, owing to the absence of spontaneous contractions, we could not be certain on this point.

We then remembered that we had made a routine practice of administering a dose of castor oil to the dogs used in our former experiments. On repeating our experiments on cats, which had received an ounce of castor oil the day before, we found that this drug had a distinct influence on the activities of the local nerve-centres. In 2 out of the 3 experiments, the local reflexes were well-marked. The intestines on exposure, after the extirpation of the abdominal ganglia, were in a state of activity and presented spontaneous peristaltic contractions. Stimulation below the balloon caused an increase in the contractions of the intestinal wall in the neighbourhood of the balloon, whereas stimulation above caused an inhibition. (Fig. 8.)

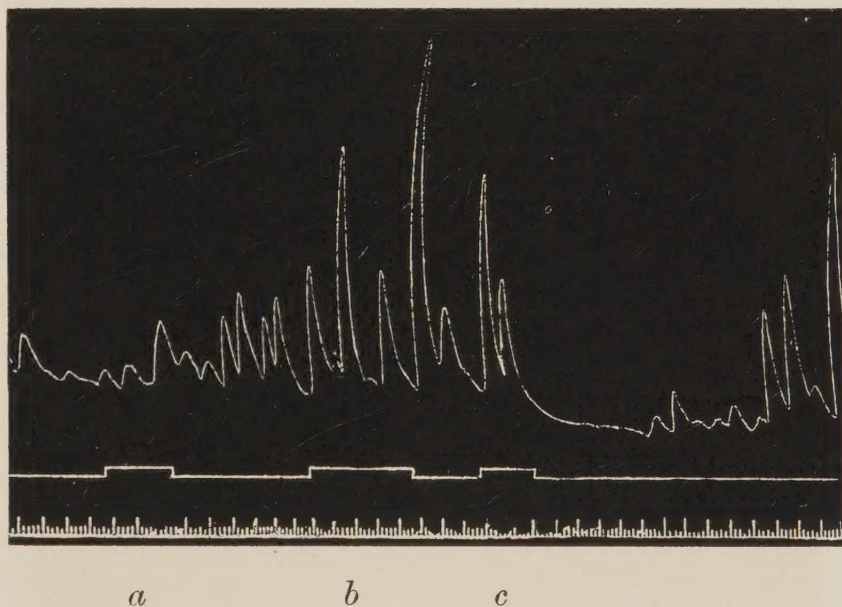


Fig. 8. Local reflexes in enervated intestine of cat. *a* and *b* intestine pinched below. At *c*, pinch above.

These results, although perfectly definite, could not be obtained with the same facility as in the dog, and any segment of gut apparently soon lost its power of local reaction on repeated stimulation. Having

gained however definite evidence of the presence of local reflexes in the cat's small intestine, we did not think it worth while to spend more time in trying to ascertain the causes of the frequent absence of these reflexes. It must be remembered in this connection that the cat is still more purely carnivorous than the dog, and therefore requires a much more seldom intestinal activity.

Extrinsic innervation of the cat's small intestine.

The action of the splanchnic and vagus nerves on the small intestine of the cat is exactly analogous to their action in the dog. Stimulation of the splanchnic nerves causes well-marked inhibition, accompanied by but not dependent on constriction of the blood vessels (Fig. 9). In no case have we observed any trace of a motor influence of these nerves on either coat of the intestine, although there may be occasionally a slight augmentation of the contractions which immediately follow

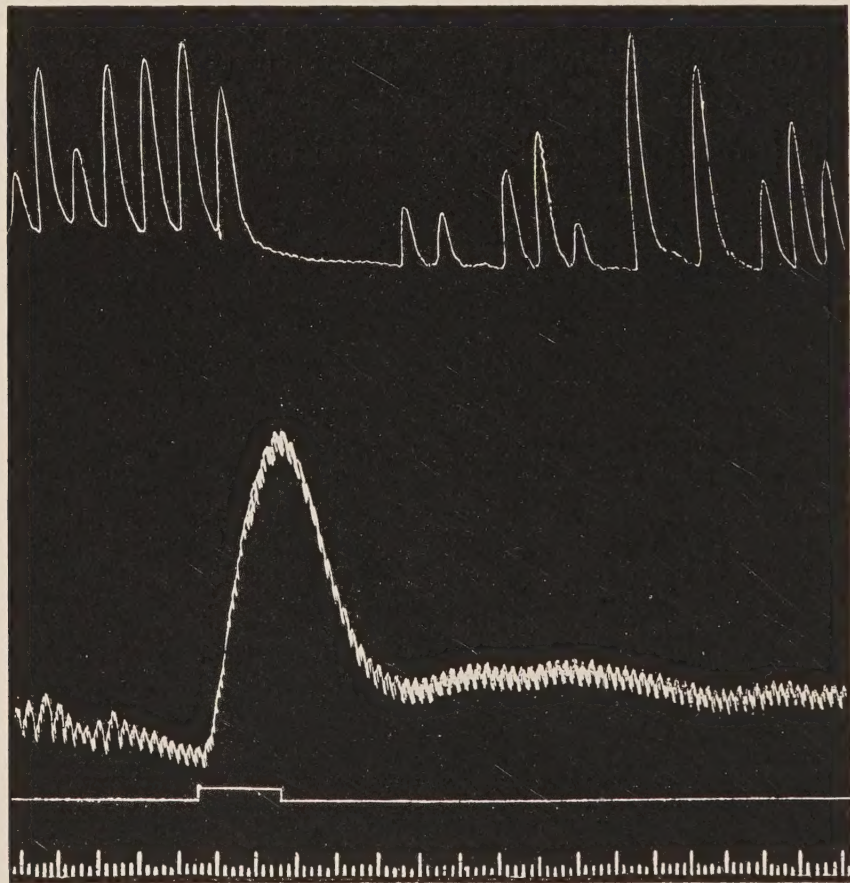


Fig. 9. Tracing to show inhibitory influence of splanchnic nerve on intestine of cat.

the inhibition. Stimulation of the mesenteric nerves has the same effect as stimulation of the splanchnic nerves (Fig. 10).

It is interesting to note that the inhibitory effect of the splanchnics as well as the motor effect of the vagi, may be obtained with com-

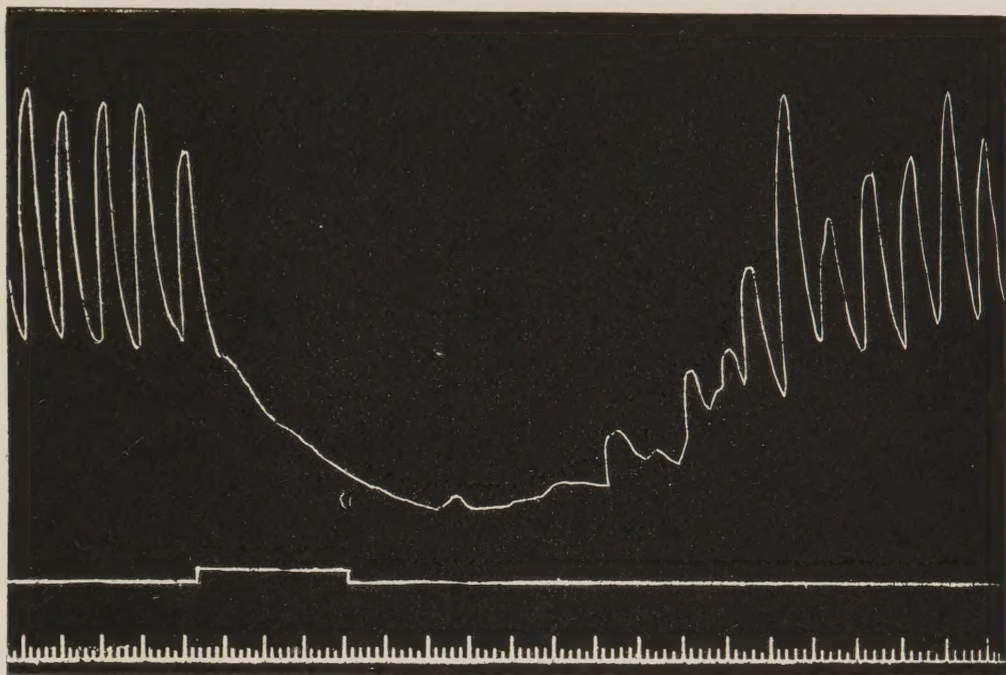


Fig. 10. Tracing of contractions of kitten's intestine, showing inhibition due to stimulation of mesenteric nerves.

parative ease in animals in which there is no trace of local reflexes. In the kitten, from which Fig. 10 was taken, the rhythmic contractions represented at the beginning of the tracing were apparently limited to, or at any rate best marked at the centre of the balloon, and could not be influenced by stimulating the intestine either above or below the balloon. This independence of extrinsic and intrinsic innervation would seem to show that the extrinsic nerves influence the muscular fibres of the gut directly, and not through the intermediation of the local nervous mechanisms contained in Auerbach's and Meissner's plexuses. This conclusion would agree also with that arrived at by Langley, viz., that the splanchnic fibres to the muscular coat of the intestine correspond to the general law in having only one cell station, which in their case is situated almost exclusively in the ganglia of the solar plexus.

The result of stimulating one vagus (after administration of atropin) is shown in Fig. 11. It will be noticed that the initial inhibition is as well marked in the cat as in the dog. The fact that it was impossible to obtain evidence of local reflexes or descending inhibition, in the experiment from which this tracing was taken, presents a serious objection to the view put forward in the last section as to the causation

of the initial vagal inhibition. This difficulty we are not at present in a position to remove.

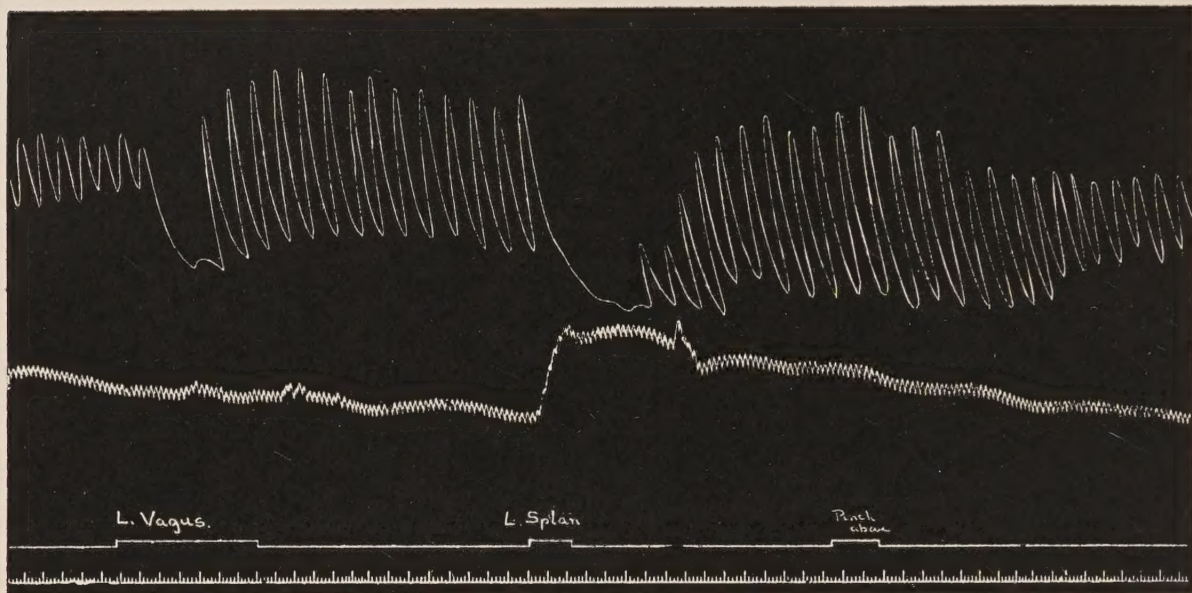


Fig. 11. Influence of vagus and splanchnic nerves on cat's intestine.

CONCLUSIONS.

1. The general laws with regard to the activity of the small intestine, previously deduced by us from experiments on dogs, are in the main applicable also to the small intestine of the rabbit and cat.

2. In both animals two kinds of activity may probably be distinguished—

(a) Myogenic rhythmic contractions ('pendulum' movements).

(b) True peristaltic contractions. These depend for their production on the activity of the local nervous structures of the intestine, as judged by the presence or absence of the local intestinal reflex (contraction above and inhibition below an excited spot).

3. The main difference between the various animals lies in the usual activity of the viscus. In the rabbit with great and constant activity, ascending excitation is very pronounced, descending inhibition very limited both in time and extent, whereas in the dog inhibition is always more easily evoked and more marked than excitation.

4. In all animals investigated the vagus acts as the motor nerve and the splanchnic as the inhibitory nerve to the small intestine (both coats). We have observed no trace of any motor action of the splanchnics on either coat.

